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² Earl of Berkeley, and Hartley, E. G. J., *London, Proc. R. Soc. (A)*, **92**, 1916 (477).

³ Loeb, J., *J. Gen. Physiol.*, **1**, 1918-19 (559).

⁴ Loeb, J., *Ibid.*, **1**, 1918-19 (483).

⁵ Loeb, J., *Ibid.*, **2**, 1919-20 (87, 273).

⁶ The influence of electrolytes on the osmotic pressure of gelatin is not due to differences in the degree of electrolytic dissociation of the gelatin salts, since, e.g. Na gelatin and Ca gelatin of the same concentration of gelatin and hydrogen ions have practically the same conductivity.⁴

⁷ Loeb, J., *J. Gen. Physiol.*, **2**, 1919-20 (173, 255); these PROCEEDINGS, **5**, 1919 (440).

⁸ Girard, P., *Paris, C. R. Acad. Sci.*, **146**, 1908 (927); **148**, 1909 (1047, 1186); **150**, 1910 (1446); **153**, 1911 (401); La pression osmotique et le mécanisme de l'osmose, *Publications de la Société de Chimie-physique*, Paris, 1912; Bernstein, J., *Electrobiologie*, 1912; Bartell, F. E., *J. Amer. Chem. Soc.*, **36**, 1914 (646); Bartell, F. E., and Hocker, C. D., *Ibid.*, **38**, 1916 (1029, 1036); Freundlich, H., *Kolloid-Zs.*, **18**, 1916 (11).

⁹ Hamburger, T., *Zs. physik. Chem.*, **92**, 1917 (385); (*Ann. Physik, Beiblätter*, **42**, 1918 (77)).

¹⁰ Perrin, J., *J. Chim. Physique*, **2**, 1904 (601); **3**, 1905 (50); *Notice sur les titres et travaux scientifiques de M. Jean Perrin*, Paris, 1918.

EVIDENCE ON THE NATURE OF NUCLEAR ACTIVITY

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Communicated by A. G. Mayor, February 10, 1920

Binuclearity hypotheses, founded in part on Richard Hertwig's chromidial hypothesis, have influenced interpretations of extra-nuclear bodies in the cytoplasm profoundly. The obvious dual capacity of the metazoan nucleus, exhibited in kinesis and interkinesis, i.e., in generative (propagatory), and somatic phases, has been made to lend itself to analogy with a true binucleate condition and to an assumption that the nucleus contains two kinds of chromatin. Of these one is supposed to be propagatory (idiochromatin), in evidence at the time of cell division, the other trophic (trophochromatin, somatochromatin), formed by the idiochromatin, but resident in the cytoplasm. This phase of the binuclearity idea is quite independent of that to which support is given by the demonstration of dimorphism in chromosomal groups during oogenesis and spermatogenesis.

The somatic phase of the nucleus covers the period during which it may be assumed that the nuclear enzymes have passed from the nucleus to the cytoplasm, and the cytoplasm has become the seat of synthetic activities. The nucleus at this time is in a "resting" condition; it seems comparatively empty, is acidophile, and basophilic granules may be found in the cytoplasm.

What is the nature of these basophilic bodies? Are they of direct or indirect nuclear origin?

The accounts of the extrusion of chromatin from the nucleus are numerous. Under the influence of the binuclearity hypothesis supposed particles

of chromatin in the cytoplasm have been interpreted as chromidia, or as trophochromidia. Schaxel (1911) in a series of able papers, has presented evidence in support of the idea of emitted chromatin; Dantchakoff's (1916) observations support the idea. On the other hand Beckwith (1914), by no means denying, and Gatenby (1919), strongly supporting the idea of emissions from the nucleus, find no evidence of the emission of *formed* materials, in the sense of filtration of chromatin through the nuclear membrane.

There have been no observations which have enabled us to link, in any satisfactory way, our theories concerning the synthetic activities of the nucleus with the observations of Chambers (1917) on reversible changes in the cytoplasm, and with other knowledge of colloidal solutions. The material on which this paper is based makes an attempt at such a linkage possible.

In 1908 (*Biol. Bull.*, 15, p. 132), in discussing sections of *Arbacia* eggs fertilized by *Moir*a sperm, an inter-ordinal cross, I wrote, "In eggs in which the daughter nuclei are in the resting condition succeeding the first division, the cytoplasm contains many deeply staining rods. The nucleus at this time does not take the chromatin stain and appears like an empty vesicular structure."

"In eggs of the same lot and on the same slides, in which the fibers of the second amphiasier have begun to form, the nucleus again takes the stain and shows the chromatic net, while the cytoplasm is seen to be free from the bodies described."

"These structures have puzzled me not a little, but I have finally reached the conclusion that the eggs in which they occur are degenerating. Even though this be true it is difficult to explain the simulation or perhaps occurrence of longitudinal and transverse divisions of these chromosomes lying free in the cytoplasm."

The facts were so unusual that in 1911 I prepared and later studied a more complete set of material. One of my graduate students, Miss Pauline Shorey, also sectioned and studied duplicate stages, but it is not until recently that I have been willing to venture an explanation.

The material comprises ten stages, taken at short intervals through a period extending from 25 minutes after insemination to 100 minutes after insemination, or through the anaphases of the third division. Unfortunately, from the point of a study of cytoplasmic inclusions in general, but especially of mitochondria, but one fixing fluid, acetic sublimate (5% acetic), was used. Nevertheless, as the straight fertilized *Arbacia* eggs used for comparison were fixed in the same way, the opportunity for a sound and logical comparison exists. The sections on which the greater part of the study was made were stained in Heidenhain's iron-haematoxylin, but for the determination of special conditions Auerbach's acid fuchsin-methyl green, basic fuchsin, basic fuchsin-methylen

blue, saffranin-gentian violet, thionin, and some of the carmine stains were used.

In the sections of the *Arbacia-Moira* material a cycle of changes may be noted, changes concerned with the appearance and disappearance of basophilic bodies in the cytoplasm. The development of these bodies may be followed as they appear in a cloud outside of the nucleus, then in lines radiating from the nucleus, then scattered irregularly in the cytoplasm, the nucleus during this time being in the resting condition.

The basophilic bodies appear first in the form of fine granules in the immediate vicinity of the nucleus, then as short rods, which may be seen either singly or in short chains throughout the cytoplasm. These rods are of about the thickness and length of the chromosomes of *Arbacia*.

A study of the nucleus in the sections of the eggs of this period reveals the fact that the nucleoli have become much paler. In the earlier stages they stain uniformly; in the later the surface (rim in the sections), only stains, while the center remains clear. Deeply stained granules may be seen aggregated at the inner surface of the nuclear membrane as though adsorption were taking place. In some sections a massing of granules may be seen at one side of the nucleus, this mass probably being the expanded chromatin of the male nucleus. There is a distinct impression of diffusion from the nucleus, but there is no evidence of the emission of chromatin as such. At the end of this stage the nucleus is distinctly acidophile.

Then a reversal of the process begins. The sections give the impression of a movement of some of the contents of the cell toward the nucleus; again there is the appearance of a diffuse cloud in the region of the nucleus; the number of rods becomes distinctly smaller, until in the late prophase the cytoplasm has cleared almost completely. The nucleus becomes increasingly basophilic as it passes into the prophase of division. The nucleus increases in size. In the metaphase and in the anaphases of division the cytoplasm is free from rods. During this stage there is no visible evidence of the passage of materials through the nuclear membrane and into the nucleus, but the nuclear content has distinctly increased.

If we correlate these facts with the conditions shown by Chambers to exist in the egg at this time, we find that the diffuse cloud appears while the nucleus is lying in the liquid hyaloplasm sphere. This is at the beginning of the "pause" Wilson (1895), succeeding the fusion of the nuclei in fertilization. The sudden appearance of granules and then of rods indicates a rapid diffusion of enzyme throughout the cell. The rods are very numerous at this time and lie without definite orientation in the cytoplasm. M. R. Lewis determined for Chambers that diffusion of cresyl-blue takes place quickly—in a few seconds—after injection within a cell. The formation of the granules and rods may be interpreted as the result of a reaction of the cytoplasm to the nuclear enzymes.

Following this stage the hyaloplasm sphere divides, as shown by Chambers, and each portion moves and lies like a cap on the nucleus at opposite poles, and the formation of the asters, accompanied by the transition to the gel phase in the cytoplasm, begins. In my material there is evidence of a centripetal flowing, as indicated in the orientation of the rods, as this reversal occurs.

What are these rods? They are not mitochondria. The acetic acid in the fixing fluid has dissolved these. They are not chromosomes. The mass and number of the rods greatly exceed that of the chromosomes. I do not believe them to be chromidia, fragments of chromatin lying freely in the cytoplasm.

I believe that they are a coarse precipitate, possibly a synthetic product, formed by the action of extruded nuclear enzymes into the cytoplasm, and that the processes that I have described are similar to those that occur normally, but which cannot be seen under ordinary conditions, for the reason that the particles ordinarily formed are below the limits of microscopic vision. Nor does there seem to be a probability that they could be distinguished from other moving colloidal particles if the living egg were to be studied with the ultra microscope. It should be emphasized that the granules and rods which are visible in this experimental material and which I have interpreted as a coarse precipitate, are not formed in the straight fertilized eggs.

Turning now to the explanation of the formation of these particles. If we were dealing with solutions of electrolytes the explanation would lie probably in the application of von Weimarn's law on the relation between concentration of the reaction mixtures to the size of the particles of the precipitate. If we compare von Weimarn's microphotographs of the precipitates of barium sulphate formed by pouring together solutions of barium cyanid and magnesium sulphate, with the sections here under consideration, a striking similarity to those obtained at concentrations of 1/500 normal to 1/50 normal will be evident. (Reproductions of some of these microphotographs may be found in Ostwald and Fischer, *Theoretical and Applied Colloid Chemistry*, pp. 27-32.)

But we are dealing with an emulsion colloid, possibly a mixture of suspensoids with emulsoids. The phenomenon that I have described, the formation of granules and rods, is clearly due to a coalescence of particles into coarsely dispersed aggregates.

It seems probable that the suspensoid particles surrounded, "protected," by emulsoid particles, coalesce, as a result of dehydration due to an enzyme emitted from the nucleus. Inasmuch as the change is reversible and these particles pass again into solution the electrical nature of the process is also probable. This naturally would be the case if we were dealing with a suspensoid fraction.

Passing from the changes shown prior to and during the first division,

it should be noted that in this material there is no further formation of rods. The coarsely granular precipitate is well marked in the second and third divisions, but no rods are formed.

It is evident that my conclusion from a study of the material described is that the basophilic bodies found are not in the nature of chromidia, but are the result of indirect nuclear activity. As to the applicability of these results to cases in which basophilic inclusions occur normally, it is impossible to say more than that such cases should be considered in the light of the evidence here given. The explanation offered for the formation of the basophilic extra nuclear bodies described is intended to be suggestive rather than conclusive. It brings together facts which have not hitherto been associated.

A more detailed paper with illustrations is forthcoming.

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A STUDY OF THE PERSISTENCE OF VISION

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Communicated by Edwin B. Wilson, February 20, 1920

Introduction.—It was observed by Allen,¹ while investigating the effect of the color of the light on the persistence of vision, that there seemed to be portions of the retina where the persistence of the retinal impression was less than on the fovea. That is, when no flickering of the color under observation was perceptible in the center of the retina, a slight movement of the eye in any direction which allowed the light to fall upon the peripheral portions of the retina was sufficient to destroy the apparent continuity of the light. Allen attempted to measure the persistence for regions on the temporal side of the retina at 10 and 20 degrees from the axis of the eye but found that the results were "too uncertain to be of any use." The writer has measured the persistence of vision for several colors within the cone whose semi-vertical angle is nearly 40 degrees. More than one hundred points on the retina within this area were observed for each color used. From these data, it is possible to construct a map of the retina showing the persistence of vision for each portion.